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Biomass Production and Phosphorus Inflow in three Perennial Herb Populations in the Basin of the Mt. Geumoh

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金烏山盆地의 三種 多年生 草本植物 個體群의 植物量生産과 燐의 流入

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ABSTRACT

Seasonal changes in pool size, inflow rates in biomass and phosphorus, and the efficiency of phosphorus use in the stand of three populations (*Helianthus tuberosus*, *Artemisia princeps* and *Phalaris arundinacea*) in the basin of the Mt. Geumoh were investigated. During the early growing period, in the three species populations, the relative size of the phosphorus pool of population was larger than that of its biomass pool, but that of the phosphorus pool of belowground part decreased more rapidly than that of its biomass pool. In the *A. princeps* and *P. arundinacea* populations, the phosphorus inflow rate was markedly high during the soil thaw in early spring and its seasonal change pattern was different from that of the biomass production rate, showing two peaks in March and June. But in the *H. tuberosus* population, the two seasonal change patterns were alike. The annual biomass production was 2283 gDM m^{-2} in the *H. tuberosus*, 1884 m^{-2} in the *A. princeps* and 1879 gDM m^{-2} in the *P. arundinacea* population, and the annual phosphorus inflow was 11.35, 9.63 and 7.60 gP m^{-2}, respectively. The *P. arundinacea* population showed the smallest LAI peak(5.4 in early June), and the largest NAR peak (36.9 gDM $m^{-2}wk^{-1}$) and RGR peak (0.15g g^{-1} wk^{-1}) among the three species populations. The seasonal change patterns in whole plant EPU of the three species populations showed the bell shape, but the annual EPU values among them were markedly different. It was noticed that the population with the highest RGR showed the highest EPU among the three species populations while the population with the lowest RGR showed the lowest EPU among them.

INTRODUCTION

It has been pointed out that, in *Solidago altissima* population, nitrogen growth (i.e., nitrogen inflow) precedes biomass growth when matter mobilization in the plant body is regarded as 'growth' (Hirose, 1971), and that, in *Lespedeza bicolor* population in the next year after sowing, the ratio of the annual maximum to the minimum of the nitrogen pool is much larger than that of the biomass pool in root, though both ratios have similar amplitudes in whole population (Song and Monsi, 1974). These suggest that the behaviour (i.e., inflow, internal translocation, and allocation to each organ, etc.) of nutrient elements may be markedly different from that of biomass in process of plant growth. However, study of the relationship between biomass and nutrient elements in terms of behaviour is scarce, and if any, it is confined mainly to the relationship between biomass and nitrogen.

In this paper, the seasonal change patterns of pool size and inflow rate of biomass and phosphorus were specified, and the difference of these patterns between biomass and phosphorus and the efficiency of phosphorus use (EPU) were discussed in three perennial herb populations (*Helianthus tuberosus* L., *Artemisia princeps* Pampan and *Phalaris arundinacea* L.) in the seminatural field of the Mt. Geumoh.

MATERIALS AND METHODS

The study site. The study site was located at 800 m altitude in the basin of the Mt. Geumoh and was 600 m west of the summit (36°30′N, 128°20′ E; 987 m altitude) (Fig. 1).

In the basin, many kinds of grasses which were supposed to appear in the early stage of secondary succession were covered and a few small marshes oriented from the artificial ponds were scattered. At the border slope of one of the marshes, the *Helianthus tuberosus, Artemisia princeps* and *Phalaris arundinacea* population were sharply distin-

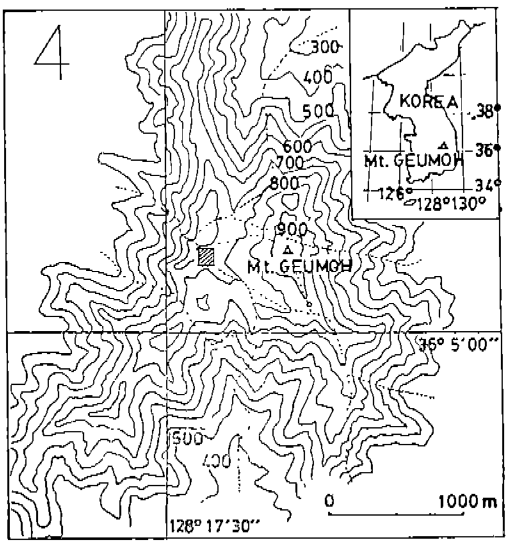

Fig. 1. Maps showing study area (shaded square mark) in Mt. Geumoh located in Gumi, Kyungpook. The dotted line represents the footpath.

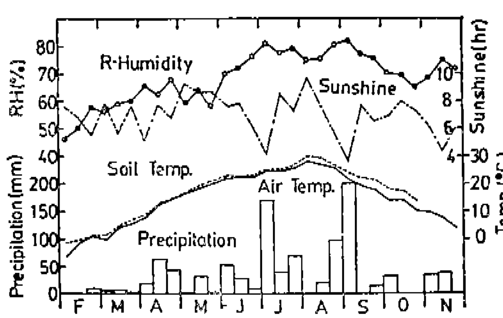

Fig. 2. Seasonal variations of mean air-and soil temperature, daily duration of sunshine and relative air humidity, and precipitation on a 10 day period. Data are after the Sunsan observatory office in 1984.

guished along the gradient of water table depth; *P. arundinacea* grew in the most wet stand, *H. tuberosus* in the least wet stand.

The soil of the sampling site was fertile loam with the variation ranges of 5~7 in pH, 0.3~0.7% in nitrogen, 0.03~0.07% in phosphorus during the growing period. The meteorological data of mean air and soil temperature, daily duration of sunshine, relative air humidity and precipitation on a 10 day period obtained from the Sunsan observatory office (1984) located about 15 km north of the Mt. Geumoh were illustrated in Fig. 2.

Sampling and phosphorus analysis. A fixed standard quadrat of 0.5×0.5 m was set in each stand of *H. tuberosus*, *A. princeps* and *P. arundinacea* populations, and then a similar sampling quadrat to the standard in density and height was selected every sampling time to avoid errors which might be arised from variability in density and plant size. Sampling was carried out in every 2 weeks from March to November, 1984.

The aboveground parts of the stand were clipped at intervals of 20 cm from the surface ground and were classified into leaf, stem and reproductive organ to take the vertical distribution diagrams (Monsi and Saeki, 1953). The belowground parts in 20 cm depth were taken and divided into the current and new parts. All samples were dried at 80 C for three days for the determination of dry matter and phosphorus analysis.

Total phosphorous of plant was measured as follows. The powdered plant samples of 50 ~100 mgDM were laid in ashes in the muffle furnace at 550~570 C for 8 hours. In order to minimize the silicate leaching from the glassware, 2 ml of 17 mM $MgSO_4$ solution was added before the ash making (Solorzano and Sharp, 1980). After appropriate diluting with distilled water, the concentration of phosphorus was determined by the ascorbic acid method (Franson, 1981) and was converted into the phosphorus fraction to plant materials.

Calculation of biomass production and phosphorus inflow. The biomass production (G_{DM} in the diagram) in each organ during every time interval (about 2 weeks) was determined by overlapping the successive two vertical distribution diagrams as exampled in Fig. 3. The G_{DM} includes not only the biomass produced by photosynthesis but also the biomass translocated from senescing or storage organs. Therefore, the biomass production in this paper represents the new growth in biomass rather than the net primary production (Hirose, 1971).

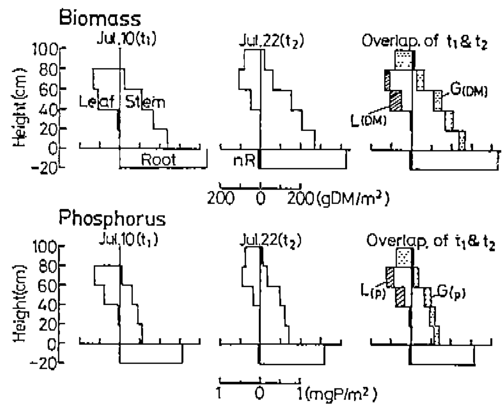

Fig. 3. The vertical distribution diagrams of biomass and phosphorus of two successive sampling times (t_1 and t_2) in *A. princeps* population, and the overlapping of these two diagrams for the determination of biomass production (G_{DM}) and phosphorus inflow (G_P). R, belowground part; nR, new belowground part; L, loss.

The phosphorus inflow (Gp in the diagram) to each organ was determined by the way applied to the determination of biomass production. The phosphorus inflow includes the phosphorus absorbed from soil and the phosphorus supplied for the growth of biomass.

RESULTS

1) Seasonal Changes of Biomass and Phosphorus Pools

Pool of biomass. In the *H. tuberosus* population, the increase of the pool of aboveground

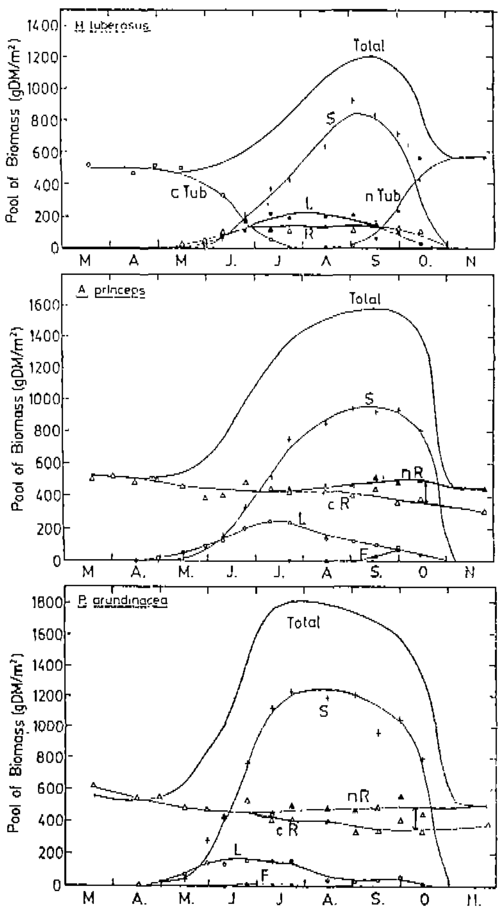

Fig. 4. Seasonal changes of the biomass pool of each organ and population in three species in Mt. Geumoh. Total, population or whole plant; L, leaf; S, stem; R, belowground part; cTub, current tuber; nTub, new tuber; F, reproductive organ; cR, current below ground part: nR, new belowground part.

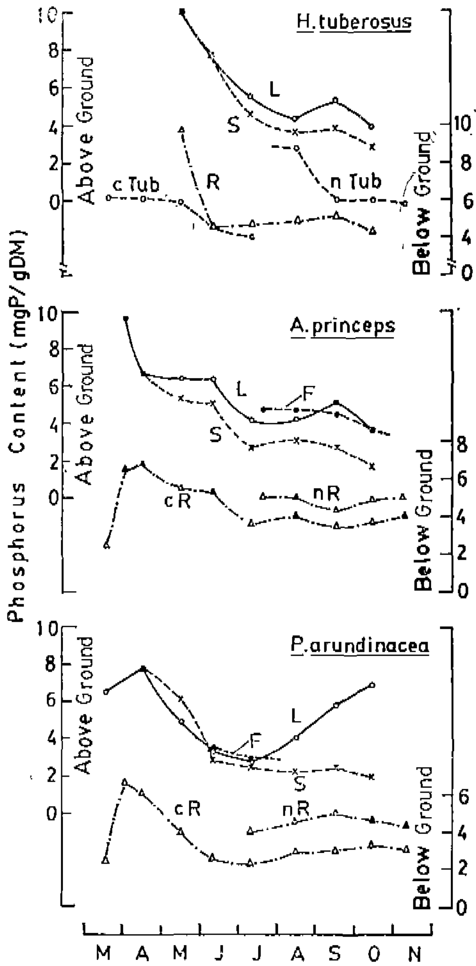

Fig. 5. Seasonal changes of the phosphorus content in each organ in three species populations. L, leaf; S, stem; R, belowground part; cTub, current tuber; nTub, new tuber; F, reproductive organ; cR, current belowground part; nR, new belowground part.

part coincided with the rapid decrease of tuber pool during the first half of growing period. It indicates that the growth of aboveground part depended on the biomass withdrawal from the tuber (Fig. 4, upper). The new tuber began to be formed in late July and increased vigorously from September with the decrease in stem biomass. The population pool ranged between 500 gDM m^{-2} in early May and 1209 gDM m^{-2} in mid-September, that is, the ratio of the maximum to the minimum pool was 2.4.

The pool of aboveground part in the *A. princeps* population began to increase in early April and the new belowground part began to be formed in mid-July. The population pool ranged between 518 $gDMm^{-2}$ in mid April and 1,580 $gDMm^{-2}$ in mid-September (Fig. 4, middle).

The population pool of the *P. arundinacea* increased vigorously from mid-May to early July. The new belowground part began to be formed from late June. The population pool ranged between 541 gDM m^{-2} in mid-April and 1,811 gDM m^{-2} in late July (Fig. 4, lower).

Content of phosphorus. In the *H. tuberosus* population, the phosphorus content in each organ decreased rapidly during the first half of the growing period (Fig. 5, upper). The variation ranges of the phosphorus content in leaf, stem and root were 3.9–10.3, 2.8–10.3 and 4.3–9.7 mgP gDM^{-1}, respectivcly. The decrease of the phosphorus content in current and new tubers may indicate that the translocation of phosphorus preceded that of biomass.

In the *A. princeps* population, the phosphorus content in aboveground part decreased during the first half of growing period with the variation ranges of 3.6–9.7 mgP gDM^{-1} in leaf and 1.7–9.7 mgP gDM^{-1} in stem (Fig. 5, middle). The phosphorus content in belowground part increased abruptly from 2.5 mgP gDM^{-1} to 6.8 mgP gDM^{-1} during the soil thaw in early spring and then the content decreased gradually in process of growth.

In the *P. arundinacea* population, the phosphorus content in leaf decreased rapidly during the first half of the growing period. After the falling down of the plant by a heavy rain in summer, the phosphorus content in the leaf which remained at the top of stem increased again in process of time (Fig. 5, lower). The seasonal variation ranges of the phosphorus content were 2.8–7.8 mgP gDM^{-1} in leaf and 2.0–7.8 mgP gDM^{-1} in stem. The phosphorus content in belowground part increased abruptly from 2.5 mgP gDM^{-1} to 6.6 mgP gDM^{-1} during the soil thaw in early spring. Though the increase of phosphorus content in shoot of a few *Erica cinerea* (Marrs, 1978), *Typha latifolia* and *Scirpus americanus* (Body, 1970) in spring was reported, it was not so dramatic as to that in the belowground part of the *A. princeps* and *P. arundinacea* populations. The decrease of phosphorus content in each organ in process of growth has been considered to be a dilution effect caused by shoot elongation (Hirose, 1974; Karlen and Whitney, 1980).

Pool of phosphorus. Phosphorus pool was obtained by multiplying the biomass by the phosphorus content. In the *H. tuberosus* population, the phosphorus pool increased from 2.75 gP m^{-2} in late May to 5.20 gP m^{-2} in mid-September. The ratio of the maximum to the minimum of the phosphorus pool was 1.9, which was lower as compared with that of the biomass pool (2.4) (Fig. 6, upper). The characteristic seasonal change of the phosphorus pool of tuber indicates that a large amount of phosphorus stored in the tuber was translocated to the aboveground part and root during the first half of the growing period, whereas a large amount of phosphorus in the aboveground part was drawn into the new tuber during the second half of the growing period. The seasonal change pattern of the phosphorus pool of each organ was similar to that of the biomass pool.

In the *A. princeps* population, the phosphorus pool ranged between 1.29 gP m^{-2} in mid-March and 5.32 gP m^{-2} in mid-August. The ratio of the maximum to the minimum of the phosphorus pool was about 4.1, which was larger than that of the biomass pool (3.1) (Fig. 6, middle). The sudden increase in early spring in phosphorus pool of belowground part may due to the rapid uptake of phosphorus from soil during the soil thaw.

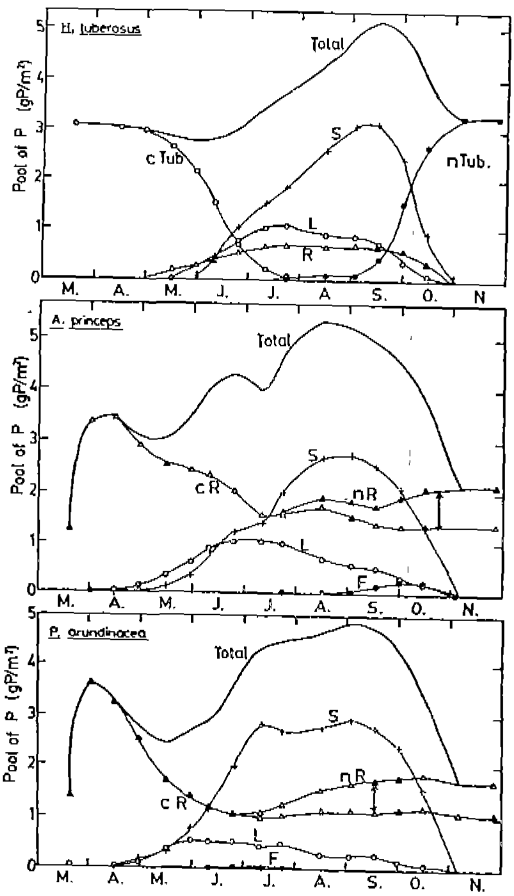

Fig. 6. Seasonal changes of he phosphorus pool of each organ and populatiton in three species populations in Mt. Geumoh. Total, population or whole plant; L, leaf; S, stem; R, belowground part; cTub, current tuber; nTub, new tuber; F, reproductive organ; cR, current belowground part; nR, new belowground part.

In the *P. arundinacea* population, the phosphorus pool ranged between 1.38 gP m^{-2} in mid-March and 4.85 gP m^{-2} in early September. The ratio of the maximum to the minimum of the phosphorus pool, 3.5, was similar to that of the biomass pool (3.4) (Fig. 6, lower). The sudden increase in phosphorus pool of belowground part occurred in early spring.

2) Biomass Production and Phosphorus Inflow

Biomass production. In the *H. tuberosus* population, the maximum rate in biomass production was 141 gDM m^{-2} wk^{-1} in mid-June (Fig. 7, upper), and the high rate in early and late stage of the growing period was considered to be the result of the high rate in biomass translocation from the tuber to the growing organs and from the aboveground part to the new tuber, respectively. The annual biomass production of the population was 2,283 gDM m^{-2}. The net assimilation rate (NAR) and relative growth

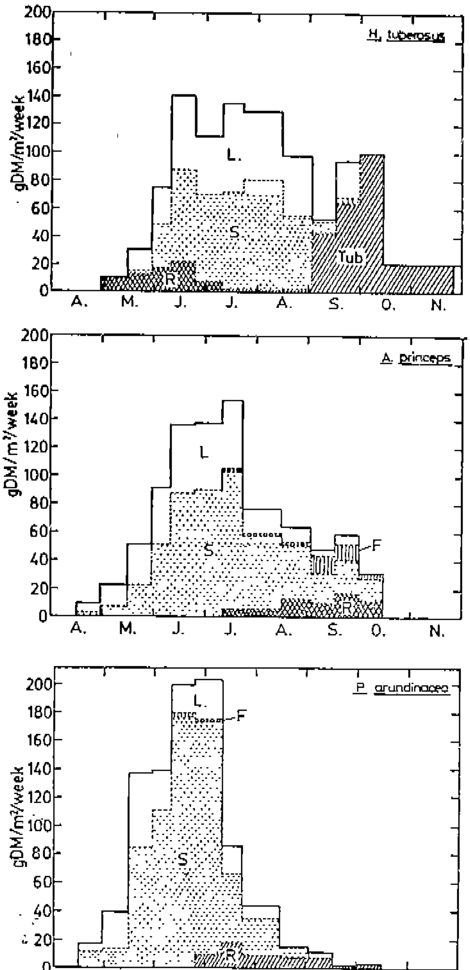

Fig. 7. Seasonal changes of the rate of biomass production in three species populations in Mt. Geumoh. L, S, R and Tub represent the weekly biomass production in leaf, stem, belowground part and tuber, respectively.

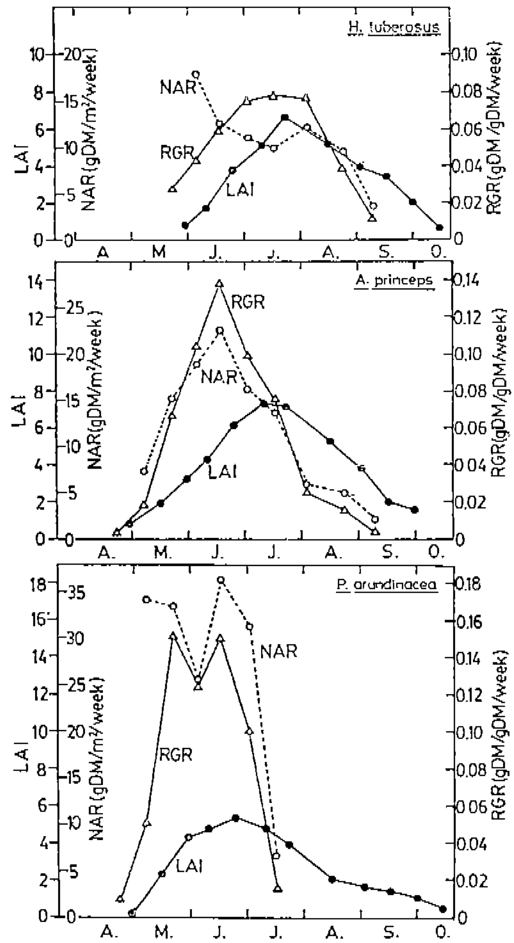

Fig. 8. Seasonal changes of the leaf area index (LAI), net assimilation rate(NAR) and relative growth rate(RGR) in three species populations in Mt. Geumoh.

rate (RGR) during the vigorous growing period (June-August) was 10.3-12.7 gDM m^{-2} wk^{-1} and 0.06-0.08 g g^{-1} wk^{-1}, respectively, and the maximum leaf area index (LAI) was 6.7 in late July (Fig. 8, upper).

In the *A. princeps* population, the maximum rate in biomass production was 153.5 gDM m^{-2} wk^{-1} in mid-July (Fig. 7, middle), and the annual biomass production was 1,884 gDM m^{-2}. The maximum LAI (7.3, in early July) of the population was not much different from that of the *H. tuberosus* population, but the NAR (15.3-22.7 gDM m^{-2} wk^{-1}) and RGR

(0.10–0.14 g g^{-1} wk^{-1}) during the vigorous growing period (May-July) were higher than those of the *H. tuberosus* population (Fig. 8, middle).

In the *P. arundinacea* population, the maximum rate in biomass production was 204 gDM m^{-2} wk^{-1} in late June, which was higher than that of the other two species populations (Fig. 7, lower). The annual biomass production of the population was 1,879 gDM m^{-2}. The NAR (25.6–36.7 gDM m^{-2} wk^{-1}) and RGR (0.12–0.15 g g^{-1} wk^{-1}) of the population during the vigorous growing period were highest among the three species populations while the maximum LAI (5.4 in early June) was lowest among them (Fig. 8, lower).

Phosphorus inflow. In the *H. tuberosus* population, the seasonal change pattern of phosphorus inflow rate was similar to that of biomass production rate showing two peaks in early and late stage of the growing period (Fig. 9. upper). The maximum rate in phosphorus inflow of the population was 0.71 gP m^{-2} wk^{-1} in early June, and the annual amount of phosphorus inflow to each organ was 11.35 gP m^{-2}.

In the *A. princeps* population, the seasonal change pattern of phosphorus inflow rate was different from that of biomass production rate showing two peaks, 0.55 gP m^{-2} wk^{-1} in early spring and 0.51 gP m^{-2} wk^{-1} in early June (Fig. 9, middle). The annual amount of phosphorus inflow to each organ was 9.63 gP m^{-2}. The amount of phosphorus inflow to the belowground part during the soil thaw in early spring was 22.9% of the amount of annual phosphorus inflow.

In the *P. arundinacea* population, the seasonal change pattern of phosphorus inflow rate was also different from that of biomass production rate showing two peaks, 0.50 gP m^{-2} wk^{-1} in late June and 0.48 gPm^{-2} wk^{-1} in early spring (Fig. 9, lower). The annual amount of phosphorus inflow to each organ of the population was 7.60 gP m^{-2}, and the amount of phosphorus inflow to the belowground part during the soil thaw was 25.4 % of the amount of annual phosphorus inflow.

3) Efficiency of Phosphorus Use

The efficiency of phosphorus use (EPU) was determined by dividing the biomass produced in each organ by the phosphorus allocated to each organ. The EPU in aboveground parts in the three species populations increased buring the first half of the growing period (Fig. 10, upper). The difference in annual EPU among different organs in the same species was large. The three species populations showed the lower values (147–166) in underground storage organ, the middle values (186–262) in leaf and the higher values (256–399) in stem. The pattern of the seasonal changes in whole plant EPU in the three species populations showed the bell shape, that is, the EPU increased gradually during the first half of the growing period and decreased during the second half of the growing period (Fig. 10, lower). But the seasonal variation ranges of the whole plant EPU were markedly different among the three species populations, showing 103–270 in the *H. tuberosus*, 161–311 in the *A. princeps*, and 97–464 in the *P. arundinacea* population.

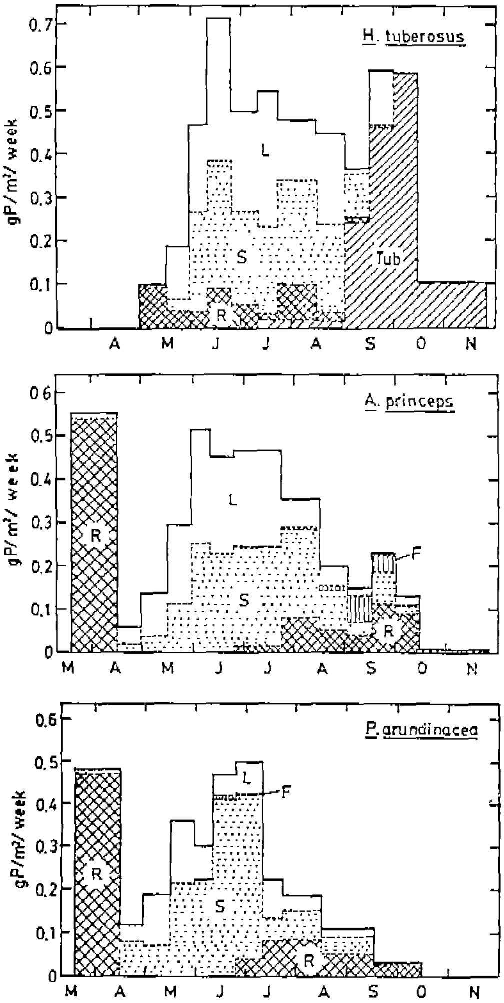

Fig. 9. Seasonal changes of the inflow rate of phosphorus in three species populations in Mt. Geumoh. L, S, R and Tub represent the weekly phosphorus inflow to leaf, stem, belowground part and tuber, respectively.

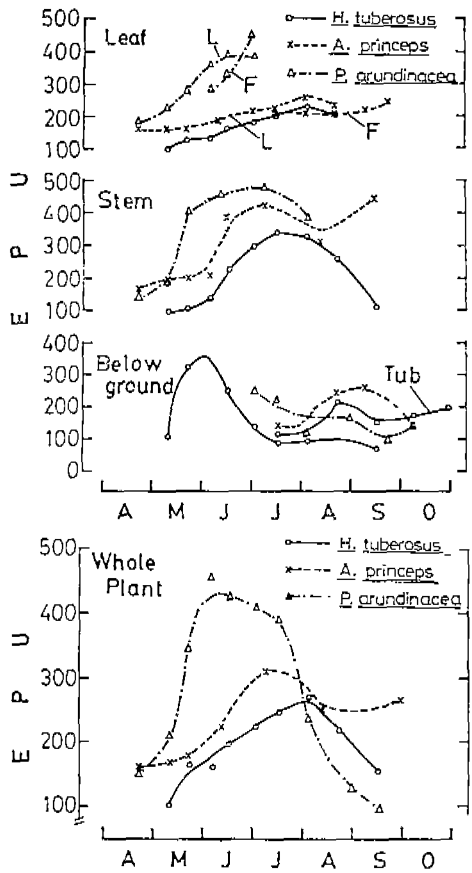

Fig. 10. Seasonal changes of the efficiency of phosphorus use (EPU) in each organ (upper) and in whole plant (lower) in three species populations in Mt. Geumoh. L, leaf; F, reproductive organ; Tub, tuber.

DISCUSSION

The difference between biomass and phosphorus pool in seasonal change pattern was conspicuous. In the early spring, the phosphorus pool of the *A. princeps* and *P. arundinacea* populations was enlarged suddenly, showing as much as 66 and 75 % of the maximum pool size, respectively, while the biomass pool at that time was only 33 and 30 % of the maximum

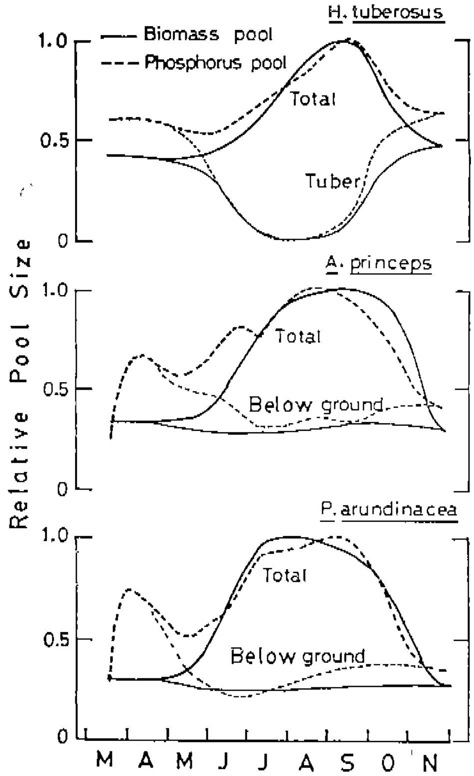

Fig. 11. Seasonal changes of relative pool size of biomass and phosphours in three species populations in Mt. Geumoh. Total, pool of population Belowground, pool of belowground part.

pool size, respectively (Fig. 11). In the *H. tuberosus* population, the phosphorus pool in early spring was 60 % of the maximum pool size, while the biomass pool at that time was only 41 %. This phenomenon seemed to have a considerable ecological significance, because an inadequate supply of nutrient might restrict the biomass production from the first growing stage. The decrease of phosphorus pool after the sudden increase of it in the *A. princeps* and *P. arundinacea* populations might result from the phosphorus absorption in excess of requirement. The phosphorus pool of belowground part decreased far more rapidly than its biomass pool in the three species populations. This result indicated that the phosphrus stored in the belowround part was translocated to the other growing parts far more rapidly than the biomass.

The preparation of phosphorus for the future growth in the three species populations was accomplished by a characteristic way. That was, the *H. tuberosus* population prepared a great deal of phosphorus by forming new tuber during the second half of the growing period, while the *A. princeps* and *P. arundinacea* populations, though they had rhizomes as a storage organ, prepared a great deal of phosphorus by the rapid absorption from the soil in early spring. And it was found that, when phosphorus inflow and biomass production were accumulated respectively in process of time, the increase in accumulation percentage of phosphorus inflow preceded by far that of biomass production in the *A.princeps* and *P. arundinacea* population, while the two increase patterns were alike in *H. tuberosus* population (Fig. 12).

The absorption rate of phosphorus including other nutrients is known to be closely correlated with the internal concentration as well as nutrient availability (Greenway, 1968; Chapin et al., 1982). That is, increase in absorption rate is due to enhanced delivery of ions to the sites of uptake, and is induced by a decrease in internal concentration. And, the phosphorus solubility, soil water content and diffusion rate of nutrient through soil are also the major controls on rate of uptake by the active fraction of the live root (Cole *et al.*, 1977; Larcher, 1980). From these suggestions, it can be supposed that the flush of soil phosphorus and increase in soil water potential, which may resulted from the surface soil thaw, and the lowest level of phosphorus content in belowground part before the soil thaw make these two species populations (i.e., *A. princeps* and *P. arundinacea*) possible to absorb phosphorus abruptly in early spring.

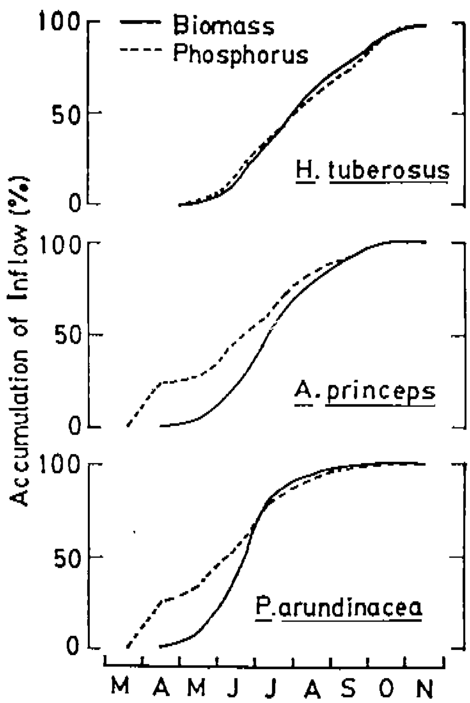

Fig. 12. The increase of the accumulation percentage of biomass production and phosphorus inflow in three species populations in Mt. Geumoh.

The annual EPUs of whole plant of the three species populations, were much different, showing 201 in the *H. tuberosus*, 254 in the *A. princeps* and 331 in the *P. arundinacea* population. This value was by far lower than that in the other species reported, which was 655 in the maize plant population in temperate culturing field (Huque and Song, 1981), 670 in the *Aconitum japonicum* population in Mt. Hakkoda (Midorikawa, 1959), 1200 in the *Arundinella hirta*-type community and 1420 in the *Miscanthus sinensis*-type community in the Kirigamine montane grasslands (Hirose, 1974). From the fact that the annual value, the variation ranges of the three and the maximum value of EPU species populations were much different among them in the similar soil condition, it could be concluded that the EPU was quite species-specific.

On the other hand, the EPU of the three species populations cultured in the soil of the extractable phosphorus content of 0.001~0.002% during the period of May-August was 280-330 in the *H. tuberosus*, 422-559 in the *A. princeps* and 496-635 in the *P. arundinacea* population. These were 1.3-1.5, 1.7-2.2 and 1.3-1.7 fold higher values respectively, as compared with the EPU of the same species population in the seminatural field of Mt. Geumoh during the same period, the soil of which had a higher extractable phosphorus content (0.03-0.07%) than the soil of the experimental culture stand. This result indicates that the EPU in the three species populations is influenced by the soil phosphorus availability, that is the EPU increases to some extent as the phosphorus availability decreases in the same species population. The same suggestion was also reported in researches on the other plants; the forest ecosystem (Vitousek, 1982 and 1984), mediterranean-type shrubs (Gray and Schlesinger, 1983) and New Zealnd alpine grasses grown in controlled phosphorus availability (Chapin *et al.*, 1982).

It has been suggested that a high efficiency of nutrient use (ENU) can be an important adaptation to nutrient stress (Loneragan and Asher, 1967; Grundon, 1972; Hirose, 1978). Contrary to this, several researchers have suggested that ENU is not an important adaptation to nutrient stress pointing out that rapidly growing species at low availabilities often show very low nutrient concentration (i.e., high efficiency) associated with visual deficiency symptoms (Clarkson, 1967; Chapin *et al.*, 1982), and that the ability of slowly growing species to maintain metabolic effectiveness under conditions of nutrient stress is a key adaptive feature (Chapin, 1980). Thus, the significance of high ENU including high EPU in the aspect of adaptation and competitional advantage to nutrient stress has not been clearly explained. However, it seems certain that the population with the highest RGR among the three species populations shows the highest EPU among them, while the population with the lowest RGR shows the lowest EPU among them.

摘　要

金烏山 盆地에 分布하는 뚱단지(*Helianthus tuberosus* L.), 쑥(*Artemisia princeps* Pampan) 및 갈풀(*Phalaris arundinacea* L.) 個體群을 對象으로 植物量(biomass)과 燐의 풀(pool)의 크기, 流入率 및 燐利用效率(EPU)의 계절변화를 考察하였다.

生長前半期의 이들 個體群의 燐풀의 상대적 크기는 植物量풀보다 컸으며, 또 이기간동안의 地下部의 燐풀은, 植物量풀보다 빠르게 감소하였다. 쑥과 갈풀個體群의 燐流入率은 6,7月에 최대값을 나타낸 植物量流入率(植物量生産率)의 계절변화와는 달리 초봄의 土壤解氷期와 6月에 각각 頂點을 보이는 계절변화를 하였다. 그러나 뚱단지個體群에서는 流入率의 계절변화가 植物量과 燐 間에 서로 유사하였다. 뚱단지, 쑥 및 갈풀 個體群의 年間 植物量生産量은 각각 2,283, 1,884 및 1,879 gDM m^{-2}였으며, 年間 燐流入量은 각각 11.35, 9.63 및 7.60 gP m^{-2}였다. 갈풀個體群의 最大 LAI는 6月 初旬에 5.4로서 세 개체군 중에서 가장 작았으나 最大 NAR 및 RGR은 각각 36.7 gDM m^{-2} wk^{-1} 및 0.15 g g^{-1} wk^{-1}로서 가장 컸다. 各 個體群의 EPU는 生長前半期에 증가하고 後半期에 감소하는 공통성을 보였다. 그러나 EPU의 계절변화폭과 年間 EPU 값은 個體群間에 서로 달랐으며, 최대 RGR값이 가장 큰 갈풀개체군에서 최대 EPU값(464)도 가장 컸다.

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